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Ecological and potential socioeconomic impacts of two globally-invasive crayfish

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Abstract

Quantifying the impacts of invasive species, relative to native analogues, is crucial for management and policy development. Two freshwater crayfish species of global concern, *Cherax quadricarinatus* and *Procambarus clarkii*, have established populations across Africa. Negative impacts on native biodiversity and socioeconomic impacts have been documented in other continents; however, there is a paucity of information on impacts from Africa and for *C. quadricarinatus*. To fill this literature gap, this study used laboratory experiments to determine potential ecological and socioeconomic impacts conferred by the crayfish species relative to a functionally similar native analogue, the river crab *Potamonautes perlatus*, on two static, but different resources. Consumption rates were derived for the three focal species consuming the macrophyte *Potamogeton nodosus* and dead *Oreochromis mossambicus* under different temperatures regimes (19 °C and 28 °C), representing summer and winter seasons in Southern Africa, with maximum feeding rate used to infer impact. *Potamogeton* represents ecologically-important nutrient cycling macrophytes, as well as crucial habitat for juvenile fish, whereas dead *O. mossambicus* was used as proxy for fish catches in artisanal gillnet fisheries often scavenged by crayfish. Consumption of both resources by all the decapods increased with temperature. However, the two invasive crayfish showed different impact trends where *P. clarkii* had a significantly higher consumption of macrophytes than the other two decapods regardless of temperature and the same trends seen, but for *C. quadricarinatus* scavenging on fish. Crayfish introductions clearly have potential for highly destructive ecological and socioeconomic impacts to invaded systems as compared to the native crabs. The disparity between resource use emphasises the necessity to use appropriate geographical and species-specific contexts to avoid erroneous conclusions from generalised risk assessments. Derived feeding rates can be used for rapid impact assessments and comparisons in other invasion cores.

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Keywords
Cherax quadricarinatus, fishery, freshwater crabs, macrophyte, *Potamonautes perlatus*, *Procambarus clarkii*, scavenging

Introduction

Invasive alien species (IAS) are widely recognised as drivers of change; thus, impetus is on predicting, quantifying and mitigating impacts across sectors whether they be positive or negative, to provide evidence for legislators (Ricciardi et al. 2013; Blackburn et al. 2014; Tickner et al. 2020; Vimercati et al. 2020). Inland waters are disproportionately at risk of invasion due to high levels of anthropogenic disturbance and lack of inclusion in major global policy and initiatives, such as the sustainable development goals, despite contributing to numerous facets, such as alleviating poverty and hunger (Lynch et al. 2020).

Ecological impacts of IAS are comparatively well described compared to other sectors, such as social or economic impacts. Yet, there remain large geographic and taxonomic gaps which must be assessed in order to compel policy-makers to prioritise IAS management (Diagne et al. 2020). African nations and rural populations globally, rely directly upon fish products for both food and nutrition security, as well as many social, cultural and economic benefits gained from the biodiverse water resources (Chan et al. 2019; Olden et al. 2020). Without suitable predictive assessments available, environmental management recommendations are often made on the basis of family level proxies or data from other geographic regions (Hawkins et al. 2015). Lack of sufficient knowledge regarding impact prediction therein puts economic, ecological and social sectors related to inland fisheries at risk of being overlooked in future policy developments, which may further exacerbate invasion impacts.

Freshwater crayfish are amongst the most notorious and destructive IAS globally (Lodge et al. 2012; Twardochleb et al. 2013; Haubrock et al. 2021). Five species of invasive crayfish have established populations in Africa (Madzivanzira et al. 2020); this is of particular concern as crayfish are phylogenetically unique in continental Africa and are, therefore, highly novel invaders (Lodge et al. 2012; Madzivanzira et al. 2020). The two most widespread and successful species: Australian redclaw crayfish *Cherax quadricarinatus* (von Martens 1868) and Louisiana red swamp crayfish *Procambarus clarkii* (Girard 1852), are spreading at a fast rate and are invasive in several ecologically- and economically-important wetlands (Madzivanzira et al. 2020, 2021c). Despite crayfish being a model ecological species and generally being shown to have broad pervasive negative impacts on both ecology and economics (Lodge et al. 2012), there are major data deficits with regards to impacts in African systems (Madzivanzira et al. 2020) and *C. quadricarinatus* impacts globally (Haubrock et al. 2021).

Crayfish impacts include the reduction of basal resources i.e. aquatic macrophytes, predation on invertebrates and reduction of amphibian and fish abundance

(Twardochleb et al. 2013; Madzivanzira et al. 2021a). *Procambarus clarkii*, in particular, has been implicated as a major driver of macrophyte reduction which can cause cascading effects on fish, bird and invertebrate abundance via direct and indirect competition for resources (both habitat and energy requirements) (Grey and Jackson 2012). Macrophyte and leaf litter breakdown is a critical step in transferring energy and nutrients from basal resources to higher trophic levels (Choi and Kim 2020). Shredding behaviour by invasive crayfish is likely to accelerate macrophyte and leaf litter breakdown (Jackson et al. 2016). Large freshwater shredders are under-represented in African systems, with freshwater crabs of the Potamonautes genus (Jackson et al. 2016) presented as the closest native trophic analogue. Potamonautid crabs are predicted to be negatively impacted as a result of crayfish invasion as functionally similar species are more likely to be competitively excluded or outcompeted (de Moor 2002; Jackson et al. 2016; Dick et al. 2017). Replacement of the native crabs by invasive crayfish will considerably alter key ecosystem services, such as fishery production and water quality (Jackson et al. 2016; Madzivanzira et al. 2021a).

Human livelihoods are also affected directly by crayfish invasions. Artisanal fishermen have reported anecdotally how crayfish affect their catches through partial consumption of fish caught on static gillnets (Weyl et al. 2017; Madzivanzira et al. 2020). This has been reported for *P. clarkii* from Lake Naivasha, Kenya and the Nile River, Egypt and for *C. quadricarinatus* in the Kafue River, Lake Kariba and Barotse floodplain, Zambia, as well as in tilapia fisheries in Mozambique (Madzivanzira et al. 2020). Partially consumed fish left in the nets are not marketable as potential buyers consider the fish to be spoilt (TCM and JS, pers. obs). Owing to the significant contribution from fisheries to livelihoods as a source of protein, income or supplementary income, as well as the wider associated value chains (Aquatic Ecosystem Services and WWF 2020), the losses associated with crayfish damage pose potential for severe and escalating costs if mitigation efforts are not undertaken. The IUCN adopted protocol for assessing ecological impact [Environmental Impact Classification for Invasive Species (EICAT)] relies upon previously documented ecological impacts (Hawkins et al. 2015). Management actions are, thus, based upon their invasion history and impacts documented elsewhere (Ricciardi et al. 2013); however, this precludes the speculative assessment of novel or potential invaders (Laverty et al. 2017). Documenting field impact can often take a prohibitively long time and many resources. Various consumption rate experiments may be carried out in the laboratory to test the broad hypothesis that invasive species incur negative effects due to more efficient resource consumption relative to a native analogue (Dickey et al. 2020). In these instances, the use of a contextually and functionally relevant analogous species is integral for generating appropriate inferences.

Therefore, we quantify resource consumption by *C. quadricarinatus* and *P. clarkii* in comparison to a native analogue, *Potamonautes perlatus* feeding on two static resources: 1) Long-leaved pondweed *Potamogeton nodosus* (Poir) and 2) dead Mozambique tilapia *Oreochromis mossambicus* (Peters 1852). Both resources are economically and ecologically important to fishery productivity and value. Macrophytes constitute

the diet of most fishery species in African freshwater systems (e.g. Red breast tilapia *Coptodon rendalli*) (Weyl and Hecht 1998) and provide spawning ground and shelter for fish (Choi and Kim 2020). Consumption rates were investigated at temperatures which are representative of field conditions (19 °C and 28 °C) as temperature is a major driver of resource assimilation patterns (Uiterwaal and DeLong 2020). Based on previous studies (see Madzivanzira et al. 2021a), we hypothesise that: 1) *P. perlatus* feeding decreases with increasing temperature, 2) *C. quadricarinatus* has an equal or higher feeding rate than *P. perlatus*, regardless of temperature, 3) *P. clarkii* increases feeding with temperature, but has a lower impact than the other focal species. The study further attempts to estimate the loss in catch in the invaded regions of the Zambezi Basin.

Materials and methods

Collections of animals

Live *C. quadricarinatus* specimens were collected from sugarcane irrigation ponds in Nkomazi, Komatipoort in the Inkomati Basin, Mpumalanga Province (-25.5°S, 31.9°E). The recommended standard gear for trapping the *C. quadricarinatus* (Madzivanzira et al. 2021b) was used. The same gear was also successfully used to catch *P. perlatus* samples from dams in the Eastern Cape (-33.3°S, 26.5°E; -33.3°S, 26.5°E).

Live *P. clarkii* crayfish samples were collected from Mimosa Dam (-27.8°S, 26.6°E) in Odendalsrus, Free State Province, South Africa. In addition to the trapping method described above, rectangular traps (63.5 × 38 cm) baited with fish heads (Barkhuizen et al., accepted) were used to capture *P. clarkii*.

All animals caught were placed in 60 litre cooler boxes with fresh water from the source, with battery-powered air pumps and transported to a biosecure laboratory at the South African Institute for Aquatic Biodiversity (SAIAB) in Makhanda where they were acclimatised to the laboratory for at least a month prior to experimentation. Water temperature was maintained at 22 ± 1 °C and the laboratory was held under a 12:12 light:dark regime with white light and total darkness. Crayfish and crabs are omnivores (Geiger et al. 2005; Gherardi 2007; Souty-Grosset and Fetzner 2016) and, hence, all animals were maintained on cabbage leaves and cultured *Eisenia* sp. worms.

Prior to the experiments, all animals were acclimatised to the desired temperature at a rate of 1 °C/day and allowed to acclimatise to the two temperatures for a week before experiments were conducted. No animals were re-used per temperature treatment for both resources.

Macrophyte consumption

Potamogeton nodosus was collected from a pond in Makhanda, South Africa. *Potamogeton nodosus* is a heterophyllous monocotyledonous aquatic plant with both floating and submerged leaves (Ryan 1985) present in most freshwater systems in Africa (Kaplan

Table 1. Morphometric averages (mean ± SE) of *Cherax quadricarinatus*, *Procambarus clarkii* and *Potamonautes perlatus* used in the macrophyte consumption and fish scavenging experiments.

Species	Experiment	CL (mm)	Mass (g)
Cherax quadricarinatus	Macrophyte	60.01 ± 1.31	68.83 ± 2.82
Procambarus clarkii	Macrophyte	56.24 ± 1.14	59.63 ± 1.22
Potamonautes perlatus	Macrophyte	53.28 ± 1.16	87.72 ± 4.92
Cherax quadricarinatus	Fish	63.20 ± 1.10	67.34 ± 2.52
Procambarus clarkii	Fish	58.62 ± 1.53	59.54 ± 1.58
Potamonautes perlatus	Fish	53.27 ± 1.02	96.29 ± 4.95

and Symoens 2005). In the lab, plant matter was rinsed thoroughly under tap water to remove any attached macroinvertebrates. To attain a reliable biomass measurement of the macrophytes, a wet – dry conversion equation was determined by drying known mass of *P. nodosus* (5, 10, 15, 20, 25. 30, 35, 40, 45 and 50 g; n = 3) in an oven at 60 °C for 24 hrs (Madsen and Bloomfield 1993; Bickel and Perrett 2015). The subsequent equation was derived, where dry mass = -0.0043 + 0.1134·wet weight (Suppl. material 1a) (Bickel and Perrett 2015).

Prior to experimentation, the pondweed was patted dry with a paper towel and weighed, then an average of 45.65 ± 0.27 g (equivalent to 5.13 ± 0.03 g dry mass) was put into each experimental tank with an animal. These animals were randomly selected from the holding tanks and patted dry before morphometric measurements were taken for each individual (Table 1). The animals were acclimatised to the experimental tanks for one hour and deprived of food for 24 hrs before the pondweed was added. The experiments were run under a 12:12 light:dark regime for 24 hrs. After the experiment, the remaining macrophytes were patted dry, weighed and dried in an oven to determine the dry weight. Control experiments were run at each temperature treatment with *P. nodosus*, but no consumers.

Fish consumption

Dead *O. mossambicus* (160.65 ± 1.26 mm, mean total length ± SE, 74.54 ± 1.59 g mean mass ± SE) were purchased from Aquaculture Innovations in Makhanda. Experimental fish were kept frozen and defrosted prior to experimentation. *Oreochromis mossambicus* is native to eastward flowing rivers of central and southern Africa (Skelton 2001). The fish species, together with other *Oreochromis* species, are commonly referred to as "breams" in the Zambezi Basin and comprise more than 50% of their catch (Tran et al. 2019). Pre-experimental treatment of animals was identical to the macrophyte experiment.

Fish were patted dry and the total length and mass for each fish was recorded. A 50 g sinker was then inserted in their guts through the mouth so that the fish sank to the bottom. The fish were then introduced to the tanks with a consumer in each tank. Controls were also run, where the dead fish were not subjected to any consumer in the experimental tank. Fishermen in the Zambezi system deploy their gillnets around 1600 hrs and retrieve them around 0600 hrs (pers. obs.).

Feeding rates of the three focal species vary with light regime (Madzivanzira et al. 2021a); therefore, to mimic natural conditions these experiments were run in dark from 1600 hrs and terminated at 0700 hrs (i.e. 15 h). At the end of the experiment, crayfish were removed and placed in respective holding tanks. The remains of the fish were removed from the water and placed in a tray with blotting paper for excess water to drip out. The sinkers were removed from the fish. The fish were patted dry and the mass was recorded as well as the parts that were eaten. The parts of fish damaged by the decapods were expressed as the proportion (%) of fish with damage '*i*' where '*i*' is the area (mouth, eyes, abdomen, fin, gut) damaged by the predator. As it was possible that one fish had several parts damaged, a single fish could have multiple damage categories.

Data analysis

There were morphometric differences between the three species (see Suppl. material 1b), but as consumption was determined per gram of consumer this does not affect the inferences. As we used dry mass as a benchmark to gauge the accuracy of macrophyte wet mass measurements, dry mass values were used for all macrophyte associated analyses.

In order to compare consumption rates between species and allow data to be relevant to field data, with respect to trends in biomass and individual size varying with time since invasion (Madzivanzira et al. 2021c), we calculated mass of resource consumed per gram of decapod per hour ($mass^{-1}$ g^{-1} h^{-1}) (1):

$$Mass^{-1} \cdot g^{-1} \cdot h^{-1} = (N_e / Mass) / T \quad (1)$$

where N_e is the dry/wet weight of resource; Mass is the mass of individual; and T is the total experimental duration.

A t-test was used determine the extent of natural loss in mass of resource before and after the experiment in the absence of a consumer for the control treatments. As resources were presented separately and dry mass of plant matter used compared to wet mass of fish, two separate generalised linear models (GLM) were used to assess resource consumption. Both GLMs used temperature and species as factors with full interaction terms. Differences between factor levels were assessed using linear contrasts and Tukey HSD.

Differences in parts of fish damaged by the consumers was analysed with 3 × 7 contingency tables and differences tested with a Chi-square test.

For both resources, the max consumption per g of predator were chosen as the most informative measure, as the respective parameters from functional response analysis are somewhat less meaningful, and this allowed for quantification of the maximum feeding rate per g of predator. The mean mass of each crayfish (Kafue River: 63.22 ± 2.05 g: Lake Kariba: 55.85 ± 1.43 g; Barotse floodplain: 37.18 ± 2.17 g) (Madzivanzira et al. 2021c) and the maximum scavenging rate per gram of *C. quadricarinatus* in 15 h (the number of hours gillnets are deployed) was used to estimate the potential

economic losses in catch in the invaded regions of the Zambezi Basin for Kafue River, Lake Kariba and Barotse floodplain. The following equations were used to calculate the economic losses due to crayfish:

$$\textit{loss per day}\ (15\ \textit{hrs}) = \textit{crayfish consumption}\ (15\ \textit{hrs}) \times \textit{crayfish mean mass} \quad (2)$$

$$\textit{monetary loss per day} = \textit{loss per day} \times \textit{US\$}\ 1.30\ (\textit{price of fish per kg}) \quad (3)$$

$$\textit{monetary loss per year} = \textit{monetary loss per day} \times 365 \quad (4)$$

The calculations were done for the low and high temperature treatments which corresponds to the low and high water flow seasons in the invaded regions, respectively.

Results

There was no significant change in resource mass ($P > 0.05$) from before to after each control experiment, at either of the temperatures; therefore, all change in resource mass is attributed to consumption.

Macrophytes consumption experiment

Temperature and species interacted significantly on the consumption rate of *P. nodosus* (Table 2), whereby consumption of all the three species was significantly higher at 28 °C than at 19 °C ($P < 0.001$) (Table 3). Voracity of *P. clarkii* on *P. nodosus* was significantly higher ($P < 0.05$) than that for *C. quadricarinatus* and *P. perlatus* at both temperatures (Fig. 1), but there was no significant difference between *C. quadricarinatus* and *P. perlatus* ($P > 0.05$).

Fish scavenging experiment

There was a significant interaction between species and temperature on consumption of *O. mossambicus* (Table 2), whereby increased temperature significantly increased

Table 2. Model terms for all factors from GLM with a quasi-Poisson error distribution used to determine differences in macrophytes consumption and fish scavenging with regards to factors "temperature" and "species", using a Type 3 ANOVA and χ^2 to report the effects.

Model term	Resource	Chi-square	df	P-value
Temperature	*P. nodosus*	64.64	1	< 0.001
Species	*P. nodosus*	37.57	2	< 0.001
Temperature × Species	*P. nodosus*	79.37	1	< 0.001
Temperature	*O. mossambicus*	85.11	1	< 0.001
Species	*O. mossambicus*	114.42	2	< 0.001
Temperature × Species	*O. mossambicus*	143.18	1	< 0.001

Table 3. Mean (±SE) consumption of macrophyte *Potamogeton nodosus* (in 24 hrs) and scavenging of fish *Oreochromis mossambicus* by *Cherax quadricarinatus*, *Procambarus clarkii* and *Potamonautes perlatus* at 19 °C and 28 °C.

Species	Temperature (°C)	Macrophyte Wet mass consumed (g)	Macrophyte Dry mass consumed (g)	Fish scavenged (g)
Cherax quadricarinatus	19	4.88 ± 0.62	0.55 ± 0.07	10.50 ± 0.66
Procambarus clarkii	19	7.29 ± 0.41	0.82 ± 0.05	6.92 ± 0.62
Potamonautes perlatus	19	3.59 ± 0.59	0.40 ± 0.07	7.59 ± 0.88
Cherax quadricarinatus	28	9.08 ± 0.62	1.02 ± 0.07	16.77 ± 0.66
Procambarus clarkii	28	11.48 ± 0.41	1.29 ± 0.05	12.89 ± 0.75
Potamonautes perlatus	28	7.79 ± 0.59	0.87 ± 0.07	13.89 ± 0.88

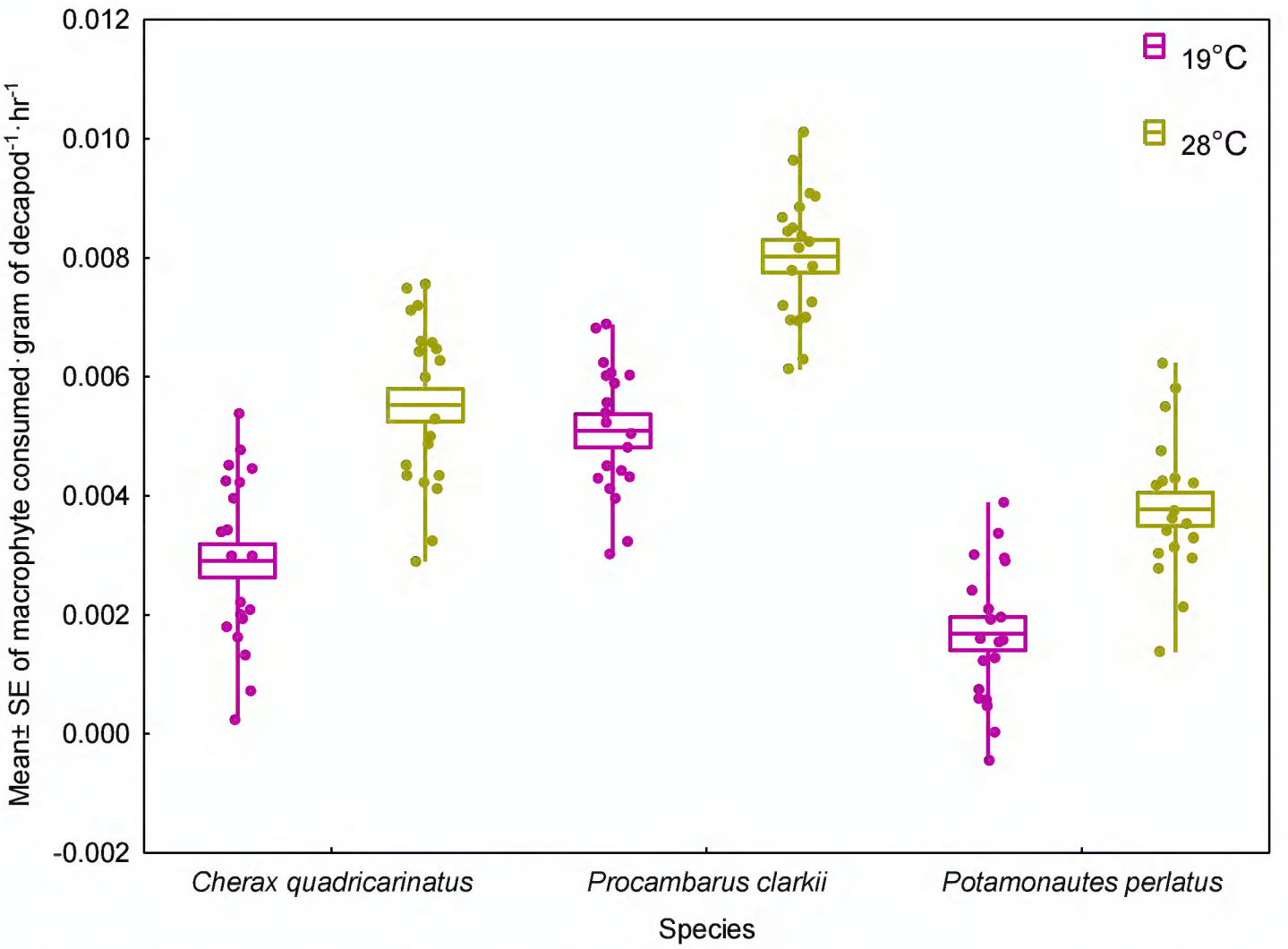

Figure 1. Mean consumption of macrophyte (*Potamogeton nodosus*) per hour per gram of *Cherax quadricarinatus*, *Procambarus clarkii* and *Potamonautes perlatus* at 19 °C and 28 °C. Points indicate raw data values, boxplots indicate ± Standard Error and solid line across the box represents the mean.

consumption of all three species ($P < 0.001$). Voracity of *C. quadricarinatus* was significantly higher (all $P < 0.05$) than that for *P. clarkii* and *P. perlatus* at either temperature (Fig. 2), but there was no difference between *P. clarkii* and *P. perlatus* voracity ($P > 0.05$).

All three decapods caused aesthetic damage to the fish through consumption (See Suppl. material 2). Each scavenger caused significantly different damage to different areas of *O. mossambicus* ($\chi^2 = 152.68$, df = 12, $P < 0.001$). The two crayfish species

Table 4. Proportion of fish with different categories of damage *i*.

Species	Temperature (°C)	Tail	Abdomen	Fin	Guts	Mouth	Head	Eyes
Cherax quadricarinatus	19	20	19	19	0	0	0	1
Procambarus clarkii	19	20	20	20	1	0	0	0
Potamonautes perlatus	19	1	4	0	0	20	20	20
Cherax quadricarinatus	28	20	17	17	3	4	0	1
Procambarus clarkii	28	20	20	20	1	0	0	0
Potamonautes perlatus	28	0	4	0	1	20	20	20

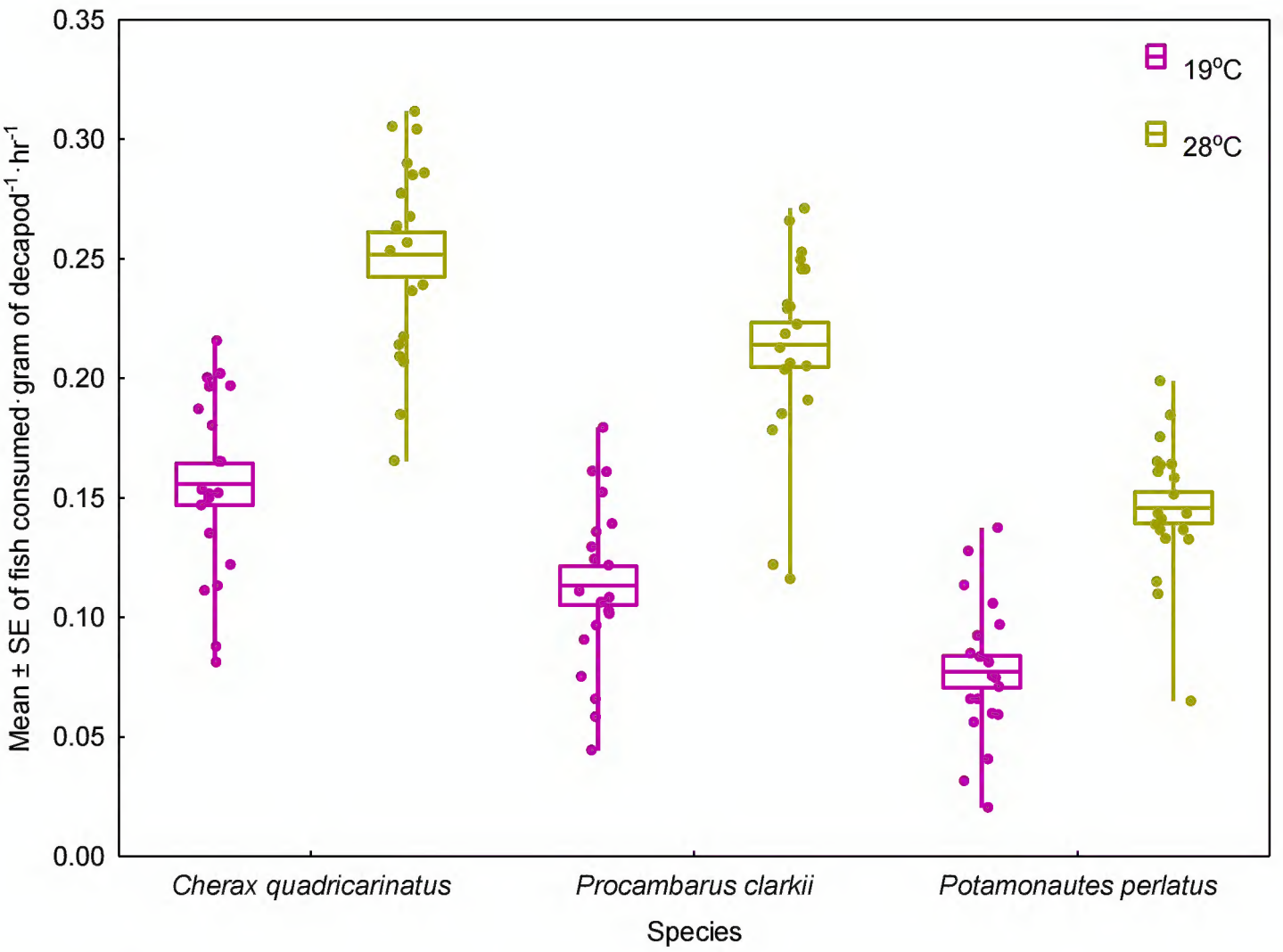

Figure 2. Mean consumption of fish (*Oreochromis mossambicus*) per hour per gram of *Cherax quadricarinatus*, *Procambarus clarkii* and *Potamonautes perlatus* at 19 °C and 28 °C. Points indicate raw data values, boxplots indicate ± Standard Error and solid line across the box represents the mean.

mostly damaged the tail, abdomen and the fins (proportion > 80%), whilst *P. perlatus* only targeted the head (proportion = 100%) (Table 4).

Potential economic losses

The potential loss in catch due to crayfish scavenging in the invasion cores per fishing night per individual crayfish ranges between: $0.01 – $0.02; $0.01 – $0.02; and $0.01 – $0.01 (Suppl. material 1). This translates to an average annual loss of $6.15; $5.42; and $3.62 per crayfish for Kafue River, Lake Kariba and Barotse floodplain, respectively (Suppl. material 1).

Discussion

High consumption of native resources, relative to that of a native analogue, is regarded as indicative of high impact IAS according to the Resource Consumption Hypothesis (Ricciardi et al. 2013; Paterson et al. 2015; Dick et al. 2017; Laverty et al. 2017). Understanding these impacts on specific ecosystem services is necessary, not only for the regulation and management of these IAS, but also to guard against detriment to human well-being, especially important in areas where food security and water resources are already precarious (Egoh et al. 2020). Here, we compare temperature- and resource-specific feeding rates by invasive crayfish and a native freshwater crab to infer ecological and potential economic impacts on fisheries. We found that consumption of static resources increases with temperature regardless of species or resource and rejected Hypothesis 1. Hypotheses 2 and 3 were also partially rejected due to species specific differences in consumption. *Cherax quadricarinatus* had a higher impact on dead fish regardless of temperature than the other two species (2) and the same trend was seen in the macrophyte experiment, but in this case, *P. clarkii* was the most damaging regardless of temperature, thus emphasising the importance of context specific impact assessments to avoid the ambiguity which arises when generalising impacts across families in the absence of species specific evidence per EICAT recommendations (Hawkins et al. 2015). The results also provide maximum feeding rates for the three decapods under two temperature treatments which can be used along with fisheries data in the future to derive potential for economic loss as well as parameterising models.

The temperature treatments in this study directly reflect the conditions in invaded African systems; however, these data can be used globally to gauge temperature-dependent impacts in other areas. Global annual mean temperatures are projected to increase by 1.5 °C between 2030 and 2052 (IPCC 2018). Thus impact of crayfish species will likely increase with the projected climatic changes, as demonstrated in this study. However, the mechanisms and outcomes of ecological impact differ depending on the crayfish species, resource type as well as native analogue dynamics as illustrated by the change in impact patterns between the present study and Madzivanzira et al. (2021a).

All species consumed *P. nodosus* and increased consumption with increasing temperature in line with the metabolic theory of ecology (Brown et al. 2004; Uiterwaal and DeLong 2020). Impact of *C. quadricarinatus* on macrophytes did not differ from that of *P. perlatus*, but *P. clarkii* showed potential for adverse ecological impacts as intense herbivory can have cascading effects across different trophic levels (Marshall 2019). The destruction of macrophytes can also modify nutrient cycling, as a result of removing the stabilising effect of macrophytes upon littoral sediments (Gherardi et al. 2011). *Procambarus clar*kii is well known for high consumption of macrophytes on a global scale (Lodge et al. 2012; Twardochleb et al. 2013; Madzivanzira et al. 2020) and exhibits a preference for plant matter over animal protein (Gherardi and Barbaresi 2007). In Lake Naivasha, the introduction of *P. clarkii* coincided with notable declines in the water lily *Nymphaea nouchalii var. caerulea* suggesting consumptive impacts on this macrophyte (Lowery and Mendes 1977). This high preference for macrophytes

by *P. clarkii* explains the difference between the comparatively low impact on juvenile fish prey in Madzivanzira et al. (2021a) and the high impact in the macrophyte experiment of the present study. The high consumption of macrophytes by *P. clarkii* could be related to feeding and processing morphology as *P. clarkii* has thin chelae and a low closing force (South et al. 2020) and a gastric mill which may specialise them for processing plant matter over other resources (Chisaka and Kozawa 2003; McGaw and Curtis 2013). *Cherax quadricarinatus* is an emerging invader with few recorded impacts (Haubrock et al. 2021). However, introductions into the Pilbara Region of Australia resulted in the complete loss of macrophyte cover and subsequent community reorganisation (Pinder et al. 2019) and, in Lake Kariba, Zimbabwe, macrophytes dominated the diet of *C. quadricarinatus* across size ranges (Marufu et al. 2018).

All three species showed propensity for scavenging behaviour on dead fish, corroborating the anecdotal accounts of crayfish destruction of fisher catch (Weyl et al. 2017; Madzivanzira et al. 2020). *Cherax quadricarinatus* consumption was more pronounced in the fish scavenging experiment, to the extent that consumption at the lowest temperature was still higher than that of *P. perlatus* at the highest temperature. The results are similar to Madzivanzira et al. (2021a) in that *C. quadricarinatus* had the highest impact on fish resources; however, *P. perlatus* did not suffer from a reduction in *per capita* consumption with increased temperature in the present study. This suggests that the results in Madzivanzira et al. (2021a) are likely due to a temperature driven mismatch in attack and escape speeds of *P. perlatus* and *Clarias gariepinus*, rather than the physiological performance of *P. perlatus* under high temperature. In contrast, *P. clarkii* had similar scavenging rates to *P. perlatus*, indicating a possible lack of impact on fish catch. However, aesthetic damage to catch often translates to economic loss regardless of extent. The two crayfish species damaged mostly the posterior parts of the fish, whilst the crabs damaged mostly the anterior parts. The fish head, preferentially damaged by the crabs, contains higher nutrient content compared to other body parts of the fish (Petricorena 2014). The higher closing force of crab chela compared to the two crayfish species may facilitate access to the anterior parts (head) of the fish which are tougher compared to the soft parts (abdomen and guts) which were more likely to be damaged by the crayfish species (South et al. 2020).

Both resource types investigated here have direct and indirect economic implications besides the ecological ramifications of generalist omnivores on aquatic communities. Healthy and high integrity macrophyte stands provide crucial fish nursery habitat and indirectly support fishery productivity and resilience (Choi and Kim 2020). The loss of macrophyte beds in Kenya due to *P. clarkii* invasion reduced food resources for a variety of African wetland birds (Taylor and Harper 1988; Harper et al. 2002) which indirectly negatively affects ornithological tourism (Gherardi et al. 2011). Inland fisheries provide livelihoods and ecosystem services for millions of people globally (Lynch et al. 2020). African artisanal fisheries suffer from pressures similar to most capture fisheries worldwide, for example, overexploitation, unemployment and rapid population growth (Tweddle et al. 2015). Fish products form part of a larger value chain commercially and when crayfish cause a percentage of the catch to be unmarketable

as a result of scavenging, targets are not met and the impacts cascade to the public, making the situation a food security cause for concern. The impact is aggrandised by low overall fish catches as crayfish entangle themselves in the gillnets, thereby reducing the efficiency of these gillnets (Weyl et al. 2017) and, further, as fishers must then increase their fishing effort to compensate for the lost catch. These dynamics might not be isolated to African systems alone (see Madzivanzira et al. 2020) and should not be underestimated. In Europe, crayfish have been shown to cause serious damage to carp rigs by clawing and nipping at the line and scavenging on bait for catching fish (see https://carp-fishing-reels.com/blog/general-advice/combatting-crayfish/). The artisanal fishery is likely to be further threatened by low catches as the crayfish species were shown to be able to consume a high number of catfish fry (Madzivanzira et al. 2021a) which could affect recruitment, productivity/yield and hence human livelihoods.

This study also estimated the potential monetary losses fishermen are likely to experience due to catch spoilage by crayfish in the invaded regions of the Zambezi Basin. The study showed high potential economic impacts in older invasions (Kafue and Lake Kariba). The potential losses in catch and income shown in this study could be even greater in the field, because the mass consumed in the lab was used to up-calculate the overall mass lost due to crayfish spoilage. This overall mass may under-represent the spoiled catch as when crayfish consume a small amount/part of the fish in the field, the whole fish is regarded as spoiled. Over- and underestimation of the losses can result in several assumptions such as that crayfish feed only on fish caught in the gillnets (overestimation in this case), not considering that small amounts consumed ruin the entire fish for sale (underestimation) and not considering fishing bans (overestimation). While this study gives a snapshot of the potential losses due to crayfish invasions, field surveys and further investigations are more appropriate to calculate the realistic losses in catch and income.

Incorporating context-specific comparisons with an ecologically relevant native trophic analogue is essential to determine the relative difference in resource consumption (Dick et al. 2017). The results of the present study show that, on a 1:1 (g) basis, the impact of both invasive crayfish is comparable to *P. perlatus* which seems to more provide evidence for possible biotic resistance (see South et al. 2020). Nonetheless, freshwater crabs, while ubiquitous across the continent, are relatively low in abundance and suffer from large data deficits in basic ecology which can confound comparative inferences (Madzivanzira et al. 2020; South et al. unpublished data). The invasion by crayfish species can lead to more diverse impacts and threaten resources that were not previously threatened by the crabs alone. We stress the need to combine laboratory data, such as the present study and Madzivanzira et al. (2021a) with contextually relevant field abundance patterns to improve prediction of impact magnitude (Dick et al. 2017; Zeng et al. 2019; Dickey et al. 2020). It is, thus, likely that the actual field impact of crayfish invasions is exacerbated by extreme differences in relative abundance between trophic analogues (South et al. 2020; Madzivanzira et al. 2021c, South et al. unpublished data). The derivation of temperature-specific per gram maximum feeding estimate for global invaders can facilitate rapid assessments and comparisons from other invasion cores which ultimately will assist in hypothesis testing and impact prediction.

Crayfish invasions have high negative implications for ecology and socio-economic dynamics of the recipient area. Intersectional adverse impacts are likely to persist and escalate, especially considering the low level of conservation management resources available (Madzivanzira et al. 2020). The pressing issue of unhindered crayfish invasions, especially in Africa, needs to be prioritised as the food security of livelihoods in invaded regions will be affected. There is need to investigate whether results from this study translate to the actual declines in catches through fish catch assessments and value chain analysis, while considering field abundance patterns. However, this relies upon interdisciplinary collaboration to compile the relevant information for robust assessment.

Data availability statement

The raw data generated and used in the analysis, as well as the data that supports the use of the temperature treatments, are publicly available at: https://doi.org/10.6084/m9.figshare.15019593.v2.

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Supplementary material 1

Macrophyte dry weight determination and morphometric averages (± SE) of used animals

Authors: Takudzwa C. Madzivanzira, Olaf L.F. Weyl, Josie South

Data type: regression analysis and morphometric measurements

Explanation note: The supplementary file shows the graph that was used for the wet – dry macrophyte weight conversion. The file also shows the mean mophometric measurements of the decapods and reports the statistics to determine their differences.

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Link: https://doi.org/10.3897/neobiota.72.71868.suppl1

Supplementary material 2

Field and laboratory photos showing crayfish damage

Authors: Takudzwa C. Madzivanzira, Olaf L.F. Weyl, Josie South

Data type: images

Explanation note: Supplentary file 2 shows photos of field and lab-based evidence of crayfish impacts on the artisanal fishery as reported in Southern Africa.

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